www.czasopisma.pan.pl PAN www.journals.pan.pl
POLSKA AKADEMIA NAUK

POLISH POLAR RESEARCH
vol. 44 no. 4, pp. 401–417 DOI: 10.24425/ppr.2023.144544

Impact of planktivorous little auks (*Alle alle*) on soil organic matter in Spitsbergen, High Arctic

Wojciech SZYMAŃSKI[1]*, Adrian ZWOLICKI[2], Katarzyna ZMUDCZYŃSKA-SKARBEK[2] and Lech STEMPNIEWICZ[2]

[1] *Institute of Geography and Spatial Management, Jagiellonian University, ul. Gronostajowa 7, 30-387 Kraków, Poland*

[2] *Department of Vertebrate Ecology and Zoology, University of Gdańsk, ul. Wita Stwosza 59, 80–308, Gdańsk, Poland*

* *corresponding author <w.szymanski@uj.edu.pl>*

Abstract: Seabirds constitute an important link between marine and terrestrial ecosystems, one of its manifestations being the transport of organic matter from the sea to breeding grounds. The main aim of our study was to determine the impact of gregarious and planktivorous little auks on the quantity and chemistry of soil organic matter along the western coast of Spitsbergen, Svalbard archipelago. Samples from the vicinity of four breeding colonies and respective controls were investigated using the elemental analyzers as well as the Fourier transform infrared spectrometer with attenuated total reflection module. The results clearly indicate that soils affected by little auks are characterized by significantly higher content of soil organic carbon, total nitrogen, water-extractable organic carbon, and water-extractable total nitrogen in comparison with those unaffected by the birds. The size of the local population of little auks appears to be the crucial factor here. The chemistry of soil organic matter in soils affected by little auks is significantly different from that in soils unaffected by the birds. This is associated with fertilization of soils via guano deposition as well as differences in the quantity and quality of vegetation cover related to aforementioned process.

Keywords: Arctic, Svalbard, soil organic carbon, total nitrogen, water-extractable organic matter, seabirds.

Introduction

Little auks (*Alle alle*) are small, gregarious and planktivorous seabirds, which are the most numerous and widely distributed avian species in the Arctic (Otero *et al.* 2018). According to the literature, their population in the Arctic is estimated to be 26–40 million breeding pairs (Egevang *et al*. 2003; Kovacs and Lydersen 2006; Zwolicki *et al*. 2016a, 2016b; González-Bergonzoni *et al*. 2017; Otero *et al*. 2018; Keslinka *et al*. 2019). The seabirds play an important role in the translocation of mineral and organic matter from the sea, where they feed, to breeding colonies on land. Little auks, due to their abundance, supply a large amount of nutrients, such as nitrogen (N) and phosphorus (P), to terrestrial ecosystems during the breeding season, and therefore are responsible for inevitable environmental changes. One of the most important impacts is substantially better development of vegetation cover at sites fertilized by bird droppings (Szymański *et al*. 2013, 2016; Skrzypek *et al*. 2015; Zwolicki *et al.* 2016a, 2016b; Szymański 2017a, 2017b). In addition, the seabirds affect the quality of vegetation and soil fauna communities (Zmudczyńska *et al*. 2012; Zawierucha *et al*. 2016) as well as the chemistry of stream and lake water occurring in the vicinity of their colonies (González-Bergonzoni *et al*. 2017).

In spite of the fact that the impact of seabirds on the terrestrial environment in the High Arctic has been quite frequently studied, very little is known about how little auks affect it in terms of the quantity and, especially, the chemistry of soil organic matter (SOM) (Szymański 2017a, 2017b; Wetterich *et al*. 2019). This is a very important issue, because climate warming, which has been observed in the Arctic in recent decades, is responsible for a substantial increase in soil temperature, deeper thawing of permafrost, and a surge in soil microbial activity (Schuur *et al*. 2015; Palmtag *et al*. 2016; Matsuoka *et al*. 2018; Biskaborn *et al.* 2019). These processes lead to higher and faster decomposition of SOM in permafrost-affected soils and a further increase in the concentration of key greenhouse gases, such as carbon dioxide (CO_2) and methane (CH_4), in the atmosphere (White *et al*. 2004; Andersen and White 2006; Kuhry *et al*. 2013; Zubrzycki *et al*. 2013; Hugelius *et al*. 2014; Moni *et al*. 2015; Schuur *et al*. 2015). However, the relationship between accumulation and decomposition of organic matter in soils depends on many factors and processes such as climate conditions, development of vegetation cover, soil thermal and moisture regime, soil type, soil texture, soil mineralogy, soil structure, quality of SOM as well as the quantity and quality of soil microorganisms (Coûteaux *et al*. 1995; Hobbie *et al*. 2000; Kögel-Knabner 2002; Limpens and Berendse 2003; Aerts 2006; Cornelissen *et al*. 2006; Hagemann and Moroni 2015). In High Arctic terrestrial ecosystems, seabirds may also play an important role in shaping the relationship between accumulation and decomposition of SOM due to the fact that they are responsible for fertilization of soils (Zwolicki *et al*. 2013; Szymański *et al*. 2016), and therefore affect tundra vegetation (Zwolicki *et al*. 2016a, 2016b), which is primary source of SOM in the High Arctic terrestrial environment. However, this issue has been unsatisfactorily addressed in the existing literature.

The main aim of this study was to determine the impact of little auks on the quantity and chemistry of SOM along the western coast of Spitsbergen, by examining four seabird colonies differing in numbers of nesting individuals. The following three hypotheses were tested: (*i*) soils affected by droppings of little auks are characterized by significantly higher content of organic carbon, total nitrogen, water-extractable organic carbon (WEOC), and water-extractable total nitrogen (WETN) than unaffected soils; (*ii*) SOM in soils affected by droppings of little auks exhibits a significantly different chemical composition than in unaffected soils; and (*iii*) size of the seabird population plays an important role in differences in SOM quantity and chemistry between soils affected and unaffected by droppings of little auks.

Study area

This study was conducted along the western coast of Spitsbergen, which is the largest island of the Svalbard archipelago (Fig. 1). Four locations, differing in terms of the size of the little auk populations, were selected for detailed studies: (*i*) southeastern facing slope of Ariekammen Mountain in the Hornsund area,

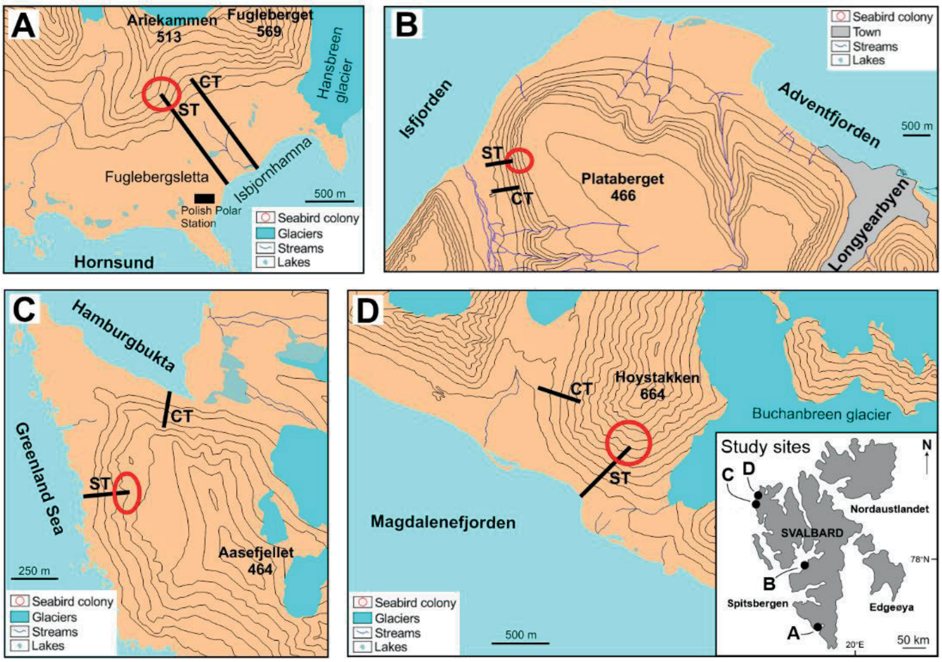

Fig. 1. Detailed location of the studied seabird (ST) and control (CT) transects in Hornsund (**A**), Isfjorden (**B**), Hamburgbukta (**C**), and Magdalenefjorden (**D**) areas.

(*ii*) northwestern facing slope of Platåberget in the Isfjorden area, (*iii*) western facing slope of Aasefjellet Mountain in the Hamburgbukta area, and (*iv*) southwestern facing slope of Høystakken Mountain in the Magdalenefjorden area (Fig. 1). The population size in the Ariekammen Mountain colony amounts to 47 000 birds, in the Platåberget colony – 500 birds, in the Aasefjellet Mountain colony – 72 000 birds, and in the Høystakken Mountain colony – 36 000 birds (Zwolicki *et al*. 2016b). The assessed mean nest density (nest m^{-2}) in Hornsund, Isfjorden, Hamburgbukta, and Magdalenefjorden colonies during soil sampling was 1.99, 0.58, 1.51, and 1.51, respectively (Keslinka *et al.* 2019). The mean annual air temperature (MAAT) in the Hornsund area is −4.2°C and total annual precipitation (TAP) is 450 mm (Marsz and Styszyńska 2007; Marsz 2013). MAAP and TAP in the Isfjorden area are −6.0°C and 190 mm, respectively (Christiansen 2005; Eckerstorfer and Christiansen 2011; Watanabe *et al*. 2017). MAAT and TAP data for the Hamburgbukta and Magdalenefjorden areas are not available; however, in the Kongsfjorden area, which is located about 70 km to the south, MAAT and TAP are −6/−7°C and 420–430 mm, respectively (Wietrzyk-Pełka *et al*. 2020).

Methods

Field methods. — Field study was conducted in July and August 2005–2010. Two transects were established at each study site, *i.e.,* Hornsund, Isfjorden, Hamburgbukta, and Magdalenefjorden (Fig. 1). The first transect was established from the seabird colony (hereafter called seabird transect) to the seashore, while the second transect was located in an area unaffected by seabirds (hereafter called control transect). The control transects were located approximately 500–1000 m from the seabird transects (Fig. 1). Each transect, depending on local geomorphology and distance of the seabird colony to the seashore, consisted of 7–12 plots (160×160 cm each) distributed at the following distances from each respective transect starting point (plot 1): plot 2 (6 m), 3 (15 m), 4 (29 m), 5 (49 m), 6 (79 m), 7 (125 m), 8 (193 m), 9 (296 m), 10 (449 m), 11 (680 m), and 12 (1026 m), as described by Zwolicki *et al*. (2013, 2016b). Soil samples from the surface layer (0–10 cm) were collected from each plot, immediately dried at 40°C using an oven, placed in plastic bags, and transported to the laboratory.

Laboratory methods. — Soil samples were gently crushed, cleaned of living roots, and sieved through a 2 mm stainless steel sieve. All the laboratory analyses were done using fine earth material (fraction < 2 mm). The content of soil organic carbon (SOC) and total nitrogen (TN) were determined using a CHN elemental analyzer (VarioMicro Cube, Elementar, Hanau, Germany) in triplicate and then averaged. An acetanilide (Merck, Darmstadt, Germany) was used as a blank in this analysis.

Ultrapure deionized water (100 ml) was added to 1 g of soil material, which had been previously ground in a mortar and shaken for 24 h, using a rotational shaker in order to prepare soil water extracts. Then the soil suspension was filtered through 0.45 μm prewashed polyethersulfone (PES) membrane filters. The prepared water extracts were used to determine the concentration of water-extractable organic carbon (WEOC), which was done by infrared detection of CO_2 after combustion of the water extracts at high temperature using a TOC analyzer (TOC-V CPN, Shimadzu). Total organic carbon CRM WC-TOC-10X-1 (AccuStandard, New Haven, USA) was used as a blank. The concentration of water-extractable total nitrogen (WETN) was determined via chemiluminescence detection of NO_x after combustion of the water extracts at high temperature by means of a TOC analyzer (TOC-V CPN, Shimadzu). Nitrate as Nitrogen IC Std 250-220-520 (SCP Science, Champlain, USA) was used as a blank.

The quality of SOM in bulk samples, which had been previously finely ground in a mortar, was determined via Fourier-transform infrared attenuated total reflectance (FTIR-ATR) spectroscopy using a Nicolet iS50 Thermo Scientific FTIR spectrometer. The FTIR spectrometer was equipped with a Pike GladiATR (Pike Technologies, Madison, WI) accessory, which allows drying samples immediately before and during analysis. The ATR crystal used was a single-reflection diamond. Samples were placed on the ATR diamond crystal, clamped with a constant force, dried at 105°C, and subsequently 32 scans with a resolution of 2 cm^{-1} from 400 to 4000 cm^{-1} were collected (Smith 2011; Ge *et al.* 2014). Each soil sample was examined in triplicate, and the spectra were averaged.

Differences in mean values of the studied soil properties, such as SOC and TN content, C/N ratio, WEOC and WETN concentration, WEOC/WETN ratio, FTIR-ATR absorbance of bands originating from organic compounds as well as ratios between the absorbance of bands between soils affected and unaffected by seabirds, in each studied location separately, and between soils from all the seabird transects combined and all the control transects combined were evaluated using the nonparametric Mann-Whitney U test, with the significance level (α) set at 0.05. All statistical calculations were performed using Statistica 13 software (StatSoft, Tulsa, OK, USA).

Results

Content of soil organic carbon and total nitrogen. — Considering all the studied seabird transects, the highest mean content of SOC and TN occurred in soils obtained from the Hornsund site (20.16% and 1.75%, respectively), and the lowest – in soils from the Isfjorden site (1.93% and 0.16%, respectively) (Table 1). Among control transects, the highest mean content of SOC and TN was obtained

Table 1.

Properties of soils from the studied transects (mean values): pH, content of soil organic carbon (SOC), total nitrogen (TN), C/N ratio as well as concentration of water-extractable organic carbon (WEOC), water-extractable total nitrogen (WETN), and WEOC/WETN ratio. Numbers in parentheses are standard errors. Asterisk indicates a statistically significant difference between a given seabird transect and its control (Mann-Whitney U test, $p < 0.05$).

Transect	pH (H_2O)	SOC (%)	TN (%)	C/N	WEOC (mg l^{-1})	WETN (mg l^{-1})	WEOC/ WETN
Hornsund							
Seabird	5.5* (0.33)	20.16* (4.26)	1.75* (0.37)	12* (0.24)	78.69* (15.73)	5.60* (1.27)	15* (0.84)
Control	7.2 (0.13)	2.18 (0.26)	0.17 (0.02)	13 (0.30)	4.99 (0.86)	0.28 (0.08)	66 (24.87)
Isfjorden							
Seabird	5.6 (0.06)	1.93 (0.21)	0.16 (0.02)	12 (0.18)	3.49 (0.53)	0.10 (0.02)	51 (11.41)
Control	5.5 (0.10)	1.94 (0.33)	0.15 (0.02)	13 (0.45)	4.39 (1.45)	0.10 (0.05)	101 (27.90)
Hamburgbukta							
Seabird	4.3* (0.06)	19.44* (3.70)	1.38* (0.23)	14* (0.47)	128.37* (22.17)	4.79* (0.83)	27* (0.96)
Control	5.2 (0.04)	6.91 (1.23)	0.60 (0.10)	11 (0.09)	49.04 (9.00)	2.61 (0.51)	19 (0.42)
Magdalenefjorden							
Seabird	4.2* (0.13)	16.35* (2.80)	1.23* (0.21)	13* (0.30)	114.43* (14.62)	6.81* (0.85)	17 (0.61)
Control	6.3 (0.10)	2.99 (0.33)	0.27 (0.03)	11 (0.16)	14.92 (2.73)	0.88 (0.14)	17 (0.66)

from soils at the Hamburgbukta site (6.91% and 0.60%, respectively) and the lowest – from the Isfjorden site (1.94% and 0.15%, respectively) (Table 1). The mean content of SOC and TN was significantly higher in soils occurring along seabird transects in comparison with mean SOC and TN content in soils found along control transects, with the exception of the Isfjorden site (Table 1).

The mean C/N ratio for soils obtained from the seabird transect was significantly lower in comparison with soils from the control transect at the Hornsund site (*i.e.,* 12 *vs.* 13) and significantly higher for the Magdalenefjorden and Hamburgbukta sites (*i.e.,* 13 *vs.* 11 and 14 *vs.* 11, respectively) (Table 1). The difference in the mean C/N ratio between soils occurring along seabird and control transects at the Isfjorden site was not significant (Table 1).

Table 2.

Properties of soils from the studied seabird transects combined and control transects combined (mean values): pH, content of soil organic carbon (SOC), total nitrogen (TN), C/N ratio as well as concentration of water-extractable organic carbon (WEOC), water-extractable total nitrogen (WETN), and WEOC/WETN ratio. Numbers in parentheses are standard errors. Asterisk indicates a statistically significant difference between a given seabird transect and its control (Mann-Whitney U test, $p < 0.05$).

Transect	pH (H_2O)	SOC (%)	TN (%)	C/N	WEOC (mg l^{-1})	WETN (mg l^{-1})	WEOC/ WETN
Seabird	4.9* (0.09)	14.91* (2.00)	1.18* (0.16)	13 (0.19)	81.05* (10.55)	4.42* (0.61)	27* (3.42)
Control	6.2 (0.08)	3.17 (0.40)	0.27 (0.03)	12 (0.20)	15.32 (3.29)	0.81 (0.18)	54 (11.78)

A comparison of the mean content of SOC and TN, and mean C/N ratio for soils collected from all the studied seabird transects combined with soils from all the control transects combined, revealed that soils affected by seabird droppings were characterized by a significantly higher mean content of SOC and TN (*i.e.,* 14.91% *vs.* 3.17% and 1.18% *vs.* 0.27%, respectively), while the difference in the mean C/N ratio for soils affected and unaffected by seabird droppings was not significant (*i.e.,* 13 *vs.* 12) (Table 2).

Concentration of water-extractable organic carbon and total nitrogen. — Considering all the studied seabird transects, the highest mean concentration of WEOC was obtained at the Hamburgbukta site (114.43 mg l^{-1}) and the lowest at the Isfjorden site (3.49 mg l^{-1}) (Table 1). The highest mean concentration of WETN obtained for all the studied seabird transects was noted in soils from the Magdalenefjorden site (6.81 mg l^{-1}) and the lowest in those from the Isfjorden site (0.10 mg l^{-1}) (Table 1). Soils occurring along the control transect at the Hamburgbukta site were characterized by the highest concentration of WEOC and WETN of all the studied control transects (49.04 mg l^{-1} and 2.61 mg l^{-1}, respectively), while soils from the control transect at the Isfjorden site exhibited the lowest mean concentration of WEOC and WETN of all the studied control transects (4.39 mg l^{-1} and 0.10 mg l^{-1}, respectively) (Table 1). The mean concentration of WEOC and WETN was significantly higher in soils occurring along seabird transects in comparison with soils from the control transects at all the studied locations with the exception of the Isfjorden site (Table 1).

The mean WEOC/WETN ratio for soils from all the studied seabird transects was the highest in the case of the Isfjorden site (51) and the lowest at the Hornsund site (15), whereas the mean WEOC/WETN ratio for soils collected from all the studied control transects was the highest at the Isfjorden site (101) and the lowest at the Magdalenefjorden site (17) (Table 1). A comparison of the mean concentration of WEOC and WETN, and mean WEOC/WETN ratio for soils collected from all the seabird transects combined with soils from all the control transects combined, indicated that soils affected by seabird droppings exhibit a significantly higher mean concentration of WEOC and WETN as well as a significantly lower mean WEOC/WETN ratio than soils not affected by droppings (Table 2).

Chemistry of SOM. — Mean FTIR-ATR spectra for the studied transects are shown in Fig. 2, while mean absorbance values of bands originating from organic compounds are presented in Table 3. The mean FTIR-ATR spectra obtained for surface soil layers occurring along seabird transects from the Hornsund, Hamburgbukta, and Magdalenefjorden sites clearly exhibited a higher intensity of bands originating from organic compounds in comparison with mean FTIR-ATR spectra obtained for surface soil layers collected from control transects (Fig. 2). Differences in the intensity of bands between soils from seabird and control transects were especially distinctive in the case of bands at ~2922 cm^{-1} (originating from aliphatic C-H groups), ~1730 cm^{-1} (originating from C=O of COOH groups and/or esters), ~1630 cm^{-1} (originating from C=C in aromatic rings and C=O of COO^{-}), ~1515 cm^{-1} (originating from C-H and N-H groups and/or aromatic C=C bonds), and ~1415 cm^{-1} (originating from C-H of aliphatic CH_2 and CH_3 groups). On the other hand, differences in the intensity of the above bands were absent in the case of soils occurring along seabird and control transects at the Isfjorden site (Fig. 2).

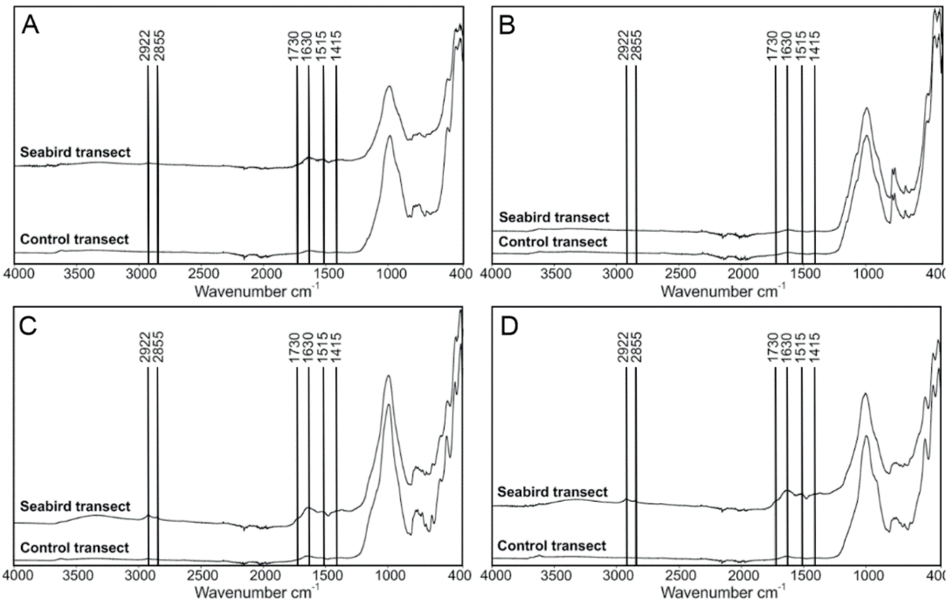

Fig. 2. Mean FTIR-ATR spectra for soil surface layer obtained from the studied seabird and control transects in Hornsund (**A**), Isfjorden (**B**), Hamburgbukta (**C**), and Magdalenefjorden (**D**) areas.

Table 3.

Mean FTIR-ATR absorbance values and ratios for bands originating from organic compounds, measured in samples from the studied transects. Numbers in parentheses are standard errors. Asterisk indicates a statistically significant difference between a given seabird transect and its control (Mann-Whitney U test, $p < 0.05$).

Transect	Mean absorbance						
	At given absorption band (cm^{-1})				As ratio between bands		
	2922	1730	1630	1515	2922/1630	2922/1730	1730/1630
Hornsund							
Seabird	0.352* (0.05)	0.188* (0.03)	0.326* (0.07)	0.265* (0.05)	1.20* (0.06)	1.92* (0.04)	0.62* (0.03)
Control	0.157 (0.01)	0.076 (0.002)	0.105 (0.004)	0.081 (0.003)	1.51 (0.003)	2.07 (0.02)	0.73 (0.02)
Isfjorden							
Seabird	0.168 (0.01)	0.076 (0.004)	0.104 (0.01)	0.079 (0.01)	1.62 (0.03)	2.22* (0.04)	0.73 (0.02)
Control	0.152 (0.01)	0.072 (0.003)	0.097 (0.004)	0.074 (0.004)	1.57 (0.04)	2.12 (0.01)	0.74 (0.02)
Hamburgbukta							
Seabird	0.352* (0.06)	0.180* (0.03)	0.280* (0.05)	0.219* (0.04)	1.29 (0.03)	1.97* (0.02)	0.65 (0.01)
Control	0.119 (0.01)	0.055 (0.01)	0.088 (0.01)	0.065 (0.01)	1.42 (0.07)	2.16 (0.01)	0.66 (0.03)
Magdalenefjorden							
Seabird	0.416* (0.05)	0.230* (0.03)	0.354* (0.05)	0.282* (0.04)	1.21* (0.04)	1.85* (0.05)	0.65 (0.02)
Control	0.110 (0.01)	0.050 (0.002)	0.079 (0.01)	0.057 (0.004)	1.40 (0.03)	2.21 (0.02)	0.64 (0.02)

Statistical analysis of mean absorbance values of bands originating from the abovementioned organic compounds indicated that soils from seabird transects at the Hornsund, Hamburgbukta, and Magdalenefjorden sites exhibited significantly higher absorbance values of bands in comparison with those in soils occurring along control transects at these sites (Table 3). In the case of the Isfjorden site, the differences were not significant (Table 3). Mean ratios of FTIR-ATR bands originating from organic compounds in the studied soils along seabird and control transects are shown in Table 3. The mean 2922/1630 ratio was lower in the case of soils occurring along the seabird transects in comparison with those in control transects, with the exception of the Isfjorden site (Table 3). However, it should be noted that differences in the mean 2922/1630 ratio between the seabird and control transects were significant only in the case of the Hornsund and Magdalenefjorden sites (Table 3). The mean 2922/1730 ratio was always significantly lower for soils obtained from seabird transects *vs.* soils collected from control transects, with the exception of the Isfjorden site. The mean 1730/1630 ratio was lower for soils obtained from seabird transects versus soils collected from control transects, with the exception of the Magdalenefjorden site (Table 3). However, differences in mean 1730/1630 ratios between soils from seabird and control transects were significant only in the case of the Hornsund site (Table 3). The results of the Mann-Whitney U test indicated that all mean FTIR-ATR ratios between bands originating from organic compounds in soils occurring in all the studied seabird transects combined were significantly lower than mean FTIR-ATR ratios for soils located along all the studied control transects combined (Table 4).

Table 4.

Mean FTIR-ATR absorbance at a given absorption band as well as mean FTIR absorbance ratios between the bands in the studied seabird transects combined and control transects combined. Numbers in parentheses are standard errors. Asterisk indicates a statistically significant difference between a given seabird transect and its control (Mann-Whitney U test, $p < 0.05$).

Transect	Mean absorbance						
	At given absorption band (cm^{-1})				As ratio between bands		
	2922	1730	1630	1515	2922/1630	2922/1730	1730/1630
Seabird	0.324* (0.03)	0.170* (0.02)	0.271* (0.03)	0.215* (0.02)	1.32* (0.03)	1.99* (0.03)	0.66* (0.01)
Control	0.136 (0.01)	0.064 (0.00)	0.092 (0.00)	0.070 (0.00)	1.49 (0.02)	2.14 (0.01)	0.70 (0.01)

Discussion

Content of SOM. — The results obtained in this study clearly indicate that soils occurring in the High Arctic and affected by seabirds such as little auks are characterized by a significantly higher content of SOC, TN, WEOC, and WETN in comparison with soils unaffected by birds. This is in agreement with our first hypothesis. The significantly higher content of SOC and TN in seabird affected soils is mainly related to the deposition of these elements with droppings and other organic wastes derived from birds (Zwolicki *et al*. 2013, 2016b; Skrzypek *et al*. 2015; Szymański *et al*. 2016). It should be noted that a clearly higher number of individuals in the colony leads to a higher content of SOC and TN in soils occurring in its vicinity (Table 1), and this is in line with our third hypothesis. A significantly higher content of SOC at sites fertilized by the seabirds is also connected with better developed vegetation cover at such sites. This is due to a higher content of nutrients, such as nitrogen and phosphorus, in the soil, which are supplied with avian guano (Zwolicki *et al*. 2013, 2016b; Skrzypek *et al*. 2015; Szymański *et al*. 2016). Zwolicki *et al*. (2016b) were able to show that the share of vascular plant cover and quantity of selected vascular plant species such as *Cerastium arcticum* and *Cochlearia groenlandica* increased with an increasing concentration of the $\delta^{15}N$ isotope derived from little auk guano in the soil.

The results obtained in this study are in agreement with those presented by Otero *et al.* (2015) and De La Peña-Lastra *et al.* (2021), who studied the impact of yellow-legged gulls (*Larus michahellis*) on soils in northwestern Spain. They reported a higher total organic carbon content in soils affected by the gulls in comparison with soils from the control site only at some locations, namely those characterized by the highest number of birds (Otero *et al.* 2015; De La Peña-Lastra *et al.* 2021). Most likely, this is related to the substantially lower number of birds occurring in the studied gulls colonies from NW Spain compared to the number of little auks in the colonies included in the present research, *i.e.,* hundreds *vs.* thousands of bird individuals (with the exception of the colony at Isfjorden site).

Significantly higher content of SOC and TN in soils fertilized by seabirds leads to a significantly higher concentration of WEOC and WETN, as both WEOC and WETN originate mainly from litter, SOM, plant roots exudates, and microbial biomass (Kalbitz *et al*. 2000; De Feudis *et al*. 2017; Szymański 2017b). The microbial decomposition of litter and SOM in the soil is responsible for the formation of WEOC and WETN (Kalbitz *et al*. 2000; McDowell 2003; Bolan *et al*. 2011; Szymański 2017b; Bartos *et al*. 2020), and therefore the higher the SOM content and soil microbial activity, the higher the WEOC and WETN concentration in the soil. Despite the fact that soil microbial activity was not determined in this study, other studies indicate that the quantity and activity of soil microorganisms (Ramsay 1983; Ramsay and Stannard 1986; Roser *et al.* 1993; Cocks *et al*. 1999), and soil fauna such as springtails (Collembola) and water bears (Tardigrada) (Zmudczyńska *et al*. 2012; Zawierucha *et al*. 2016) in soils located in the vicinity of seabird colonies, are higher in comparison with those located at sites unaffected by seabirds. Moreover, the better-developed vegetation cover at sites fertilized by seabirds is responsible for better development of the root system, and therefore a higher quantity of root exudates, which are also an important source of water-extractable organic matter (WEOM)

(Kalbitz *et al.* 2000; De Feudis *et al.* 2017). The significantly higher concentration of WEOC and WETN in soils affected by the studied seabirds in relation to those unaffected by the birds may also be connected with a lower degree of SOM binding to the mineral phase of the former soils due to their lower relative proportion between organic and mineral material, indicated by a significantly higher content of SOC (Tables 1 and 2). Additionally, it should be noted that avian guano may also serve as a direct and important source of WETN in soils located in the vicinity of a seabird colony, thus substantially increasing the concentration of WETN in them.

Chemistry of SOM. — Considering each studied location separately, mean C/N and WEOC/WETN ratios do not exhibit any clear contrast between soils affected and unaffected by the seabirds (Table 1). However, taking into account all the seabird transects combined and all the control transects combined, the mean WEOC/WETN ratio is significantly lower for soils obtained from the former transects, whereas the difference in the mean C/N ratio between the transects is not significant. This means that the WEOC/WETN ratio is a better indicator of the impact of avian guano on the quality of SOM than the C/N ratio, and this is in agreement with previous findings (Szymański 2017a, 2017b).

Results obtained in this study (via FTIR-ATR spectroscopy) indicate that the chemistry of SOM is significantly different in soils affected and unaffected by little auks, and this is in line with our second hypothesis. Soils affected by them are characterized by significantly higher FTIR-ATR absorption values of bands at ~2922 cm^{-1}, ~1730 cm^{-1}, and ~1630 cm^{-1} indicating a significantly higher content of organic compounds such as aliphatic compounds, carboxylic groups, and aromatic compounds in comparison with those not affected by seabirds. The only exception is the Isfjorden site, where the population of the studied seabirds is very small. This is related to the abovementioned reasons, notably the significantly higher content of SOC in soils affected *vs.* unaffected by birds (with the exception of the Isfjorden site) due to a higher supply of organic wastes derived from birds and better developed vegetation cover, because of a higher content of nutrients in the soil (Zwolicki *et al.* 2013, 2016b; Skrzypek *et al.* 2015; Szymański *et al.* 2016; González-Bergonzoni *et al.* 2017).

The significantly lower mean 2922/1630 and 1730/1630 ratios for soils affected by seabirds, when compared to mean ratios for soils unaffected by them, may be related to the higher degree of transformation of SOM in the former soils due to the higher abundance and higher activity of soil microorganisms and soil fauna in soils affected by seabirds (Ramsay 1983; Ramsay and Stannard 1986; Roser *et al.* 1993; Cocks *et al.* 1999; Zmudczyńska *et al.* 2012; Zawierucha *et al.* 2016). The significantly lower mean 2922/1730 ratio for soils fertilized by little auks in comparison with soil not fertilized by bird droppings is most likely related to the higher concentration of acidic COOH groups in SOM obtained from the former soils due to a significantly lower mean soil pH in relation to soil pH not affected by seabirds (Tables 1–2). The significantly lower soil pH at sites affected by seabirds is related to the biochemical transformation of seabird guano and formation of nitrate and oxalic acids (Tatur and Myrcha 1983, 1984; Tatur 1989) as well as a higher content of SOM, which provides a higher concentration of organic acids (Szymański *et al.* 2016).

The significant differences in the chemistry of SOM between soils affected and unaffected by little auks may also be related to pronounced differences in local vegetation communities as well as in the abundance of plant species. Zwolicki *et al.* (2016b) were able to demonstrate that vegetation communities at sites fertilized by little auks clearly differed from those occurring at sites not fertilized by these birds. In addition, the number of some vascular plant species and cryptogams seem also depend on the degree of soil fertilization with seabird guano, as indicated by the $\delta^{15}N$ signature in the soil (Zwolicki *et al.* 2016a). It should be noted that Szymański (2017a) used FTIR spectroscopy to demonstrate that the chemistry of selected vascular plant species and various cryptogams differs.

Conclusions

The results obtained in this study clearly indicate that soils occurring in the High Arctic and affected by little auks are characterized by a significantly higher content of SOC, TN, WEOC, and WETN in comparison with soils unaffected by the studied birds. The size of local population of little auks plays a crucial role in differences between the content of SOC, TN, WEOC, and WETN in soils located in the vicinity of seabird colonies and in soils unaffected by seabirds. The chemistry of SOM in soils affected by little auks is significantly different from that occurring in unaffected soils, and this is associated with the fertilization of soils via guano deposition as well as differences in the quantity and quality of vegetation cover related to this process. If the current rate of climate warming in the High Arctic does not slacken, the population of little auks and other seabirds breeding in this region will decrease due to the worsening of the quality of foraging areas. Undoubtedly, such a process would have a significant impact on the quantity and chemistry of SOM in High Arctic terrestrial ecosystems.

Acknowledgements. — The research was supported by a grant from the Faculty of Geography and Geology under the Strategic Programme Excellence Initiative at Jagiellonian University and the Polish Ministry of Science and Higher Education (Grant Nos. 3290/B/P01/2009/36, 1883/P01/2007/32 and IPY/25/2007) as well as the Polish-Norwegian Research Fund (Grant No. PNRF-234-AI-1/07, ALKEKONGE). The authors would like to thank the anonymous reviewers for their helpful suggestions. Language editing was done by Grzegorz Zębik.

References

Aerts R. 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94: 713–724. doi: 10.1111/j.1365-2745.2006.01142.x

Andersen S.K. and White D.M. 2006. Determining soil organic matter quality under anaerobic conditions in Arctic and Subarctic soils. *Cold Regions Science and Technology* 44: 149–158. doi: 10.1016/j.coldregions.2005.11.001

Bartos A., Szymański W. and Klimek M. 2020. Impact of conventional agriculture on the concentration and quality of water-extractable organic matter (WEOM) in the surface horizons of Retisols - A case study from the Carpathian Foothills in Poland. *Soil and Tillage Research* 204: 104750. doi: 10.1016/j.still.2020.104750

Biskaborn B.K., Smith S.L., Noetzli J., Matthes H., Vieira G., Streletskiy D.A., Schoeneich P., Romanovsky V.E., Lewkowicz A.G., Abramov A., Allard M., Boike J., Cable W.L., Christiansen H.H., Delaloye R., Diekmann B., Drozdov D., Etzelmüller B., Grosse G., Guglielmin M., Ingeman-Nielsen T., Isaksen K., Ishikawa M., Johansson M., Johannsson H., Joo A., Kaverin D., Kholodov A., Konstantinov P., Kröger T., Lambiel C., Lanckman J.-P., Luo D., Malkova G., Meiklejohn I., Moskalenko N., Oliva M., Phillips M., Ramos M., Sannel A.B.K., Sergeev D., Seybold C., Skryabin P., Vasiliev A., Wu Q., Yoshikawa K., Zheleznyak M. and Lantuit H. 2019. Permafrost is warming at a global scale. *Nature Communications* 10: 264. doi: 10.1038/s41467-018-08240-4

Bolan N.S., Adriano D.C., Kunhikrishnan A., James T., McDowell R. and Senesi N. 2011. Dissolved organic matter: biogeochemistry, dynamics, and environmental significance in soils. *Advances in Agronomy* 110: 1–75. doi: 10.1016/B978-0-12-385531-2.00001-3

Christiansen H.H. 2005. Thermal regime of ice-wedge cracking in Adventdalen. Svalbard. *Permafrost and Periglacial Processes* 16: 87–98. doi: 10.1002/ppp.523

Cocks M.P., Harris J.M., Steele W.K. and Balfour D.A. 1999. The influence of ornithogenic products on the nutrient status of soils surrounding nests in nunataks in Dronning Maud Land, Antarctica. *Polar Research* 18: 19–26. doi: 10.3402/polar.v18i1.6555

Cornelissen J.H.C., Quested H.M., van Logtestijn R.S.P., Pérez-Harguindeguy N., Gwynn-Jones D., Díaz S., Callaghan T.V., Press M.C. and Aerts R. 2006. Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia* 147: 315–326. doi: 10.1007/s00442-005-0269-z

Coûteaux M.-M., Bottner P. and Berg B. 1995. Litter decomposition, climate and litter quality. *Tree* 10: 63–66. doi: 10.1016/S0169-5347(00)88978-8

De Feudis M., Cardelli V., Massaccesi L., Hofmann D., Berns A.E., Bol R., Cocco S., Corti G. and Agnelli A. 2017. Altitude affects the quality of the water-extractable organic matter (WEOM) from rhizosphere and bulk soil in European beech forests. *Geoderma* 302: 6–13. doi: 10.1016/j.geoderma.2017.04.015

De La Peña-Lastra S., Gómez-Rodríguez C., Pérez-Alberti A., Torre F. and Otero X.L. 2021. Effects of a yellow legged gull (*Larus michahellis*) colony on soils and cliff vegetation in the Atlantic Islands of Galicia National Park (NW Spain). *Catena* 199: 105115. doi: 10.1016/j.catena.2020.105115

Eckerstorfer M. and Christiansen H.H. 2011. Topographical and meteorological control on snow avalanching in the Longyearbyen area, central Svalbard 2006–2009. *Geomorphology* 134: 186–196. doi: 10.1016/j.geomorph.2011.07.001

Egevang C., Boertmann D., Mosbech A. and Tamstorf M.P. 2003. Estimating colony area and population size of little auks *Alle alle* at Northumberland Island using aerial images. *Polar Biology* 26: 8–13. doi: 10.1007/s00300-002-0448-x

Ge Y., Thomasson J.A. and Morgan C.L.S. 2014. Mid-infrared attenuated total reflectance spectroscopy for soil carbon and particle size determination. *Geoderma* 213: 57–63. doi: 10.1016/j.geoderma.2013.07.017

González-Bergonzoni I., Johansen K.L., Mosbech A., Landkildehus F., Jeppesen E. and Davidson T.A. 2017. Small birds, big effect: the little auk (*Alle alle*) transforms high Arctic ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 284: 20162572. doi: 10.1098/rspb.2016.2572

Hagemann U. and Moroni M.T. 2015. Moss and lichen decomposition in old-growth and harvested high-boreal forests estimated using the litterbag and minicontainer methods. *Soil Biology and Biochemistry* 87: 10–24. doi: 10.1016/j.soilbio.2015.04.002

Hobbie S.E., Schimel J.P., Trumbore S.E. and Randerson J.R. 2000. Controls over carbon storage and turnover in high-latitude soils. *Global Change Biology* 6: 196–210. doi: 10.1046/j.1365-2486.2000.06021.x

Hugelius G., Strauss J., Zubrzycki S., Harden J.W., Schuur E.A.G., Ping C.L., Schirrmeister L., Grosse G., Michaelson G.J., Koven C.D., O'Donnell J.A., Elberling B., Mishra U., Camill P., Yu Z., Palmtag J. and Kuhry P. 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences* 11: 6573–6593. doi: 10.5194/Bg-11-6573-2014

Kalbitz K., Solinger S., Park J.H., Michalzik B. and Matzner E. 2000. Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Science* 165: 277–304. doi: 10.1097/00010694-200004000-00001

Keslinka L.K., Wojczulanis-Jakubas K., Jakubas D. and Neubauer G. 2019. Determinants of the little auks (*Alle alle*) breeding colony location and size in W and NW coast of Spitsbergen. *PLoS ONE* 14: e0212668. doi: 10.1371/journal.pone.0212668

Kovacs K.M. and Lydersen C. 2006. *Birds and mammals of Svalbard*. Norwegian Polar Institute, Tromsø.

Kögel-Knabner I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biology and Biochemistry* 34: 139–162. doi: 10.1016/S0038-0717(01)00158-4

Kuhry P., Grosse G., Harden J.W., Hugelius G., Koven C.D., Ping C.L., Schirrmeister R.L. and Tarnocai C. 2013. Characterisation of the permafrost carbon pool. *Permafrost and Periglacial Processes* 24: 146–155. doi: 10.1002/ppp.1782

Limpens J. and Berendse F. 2003. How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* 103: 537–547.

Marsz, A.A. 2013. Ground temperatures at Hornsund. *In*: Marsz A.A. and Styszyńska A. (eds.) *Climate and climate change at Hornsund, Svalbard*. Maritime University, Gdynia: 373–380.

Marsz A.A. and Styszyńska A. 2007. *Climate of the Polish Polar Station in Hornsund area – state, changes and their reasons*. Wydawnictwo Akademii Morskiej, Gdynia (in Polish).

Matsuoka N., Christiansen H.H. and Watanabe T. 2018. Ice-wedge polygon dynamics in Svalbard: Lessons from a decade of automated multi-sensor monitoring. *Permafrost and Periglacial Processes* 29: 210–227. doi: 10.1002/ppp.1985

McDowell W.H. 2003. Dissolved organic matter in soils-future directions and unanswered questions. *Geoderma* 113: 179–186. doi: 10.1016/s0016-7061(02)00360-9

Moni C., Lerch T.Z., de Zarruk K.K., Strand L.T., Forte C., Certini G. and Rasse D.P. 2015. Temperature response of soil organic matter mineralization in arctic soil profiles. *Soil Biology and Biochemistry* 88: 236–246. doi: 10.1016/j.soilbio.2015.05.024

Otero X.L., Tejada O., Martín-Pastor M., De la Peña S., Ferreira T.O. and Pérez-Alberti A. 2015. Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (*Larus michahellis*) in the Atlantic Islands National Park (Galicia-NW Spain). *Science of the Total Environment* 532: 383–397. doi: 10.1016/j.scitotenv.2015.06.013

Otero X.L., De La Peña-Lastra S., Pérez-Alberti A., Ferreira T.O. and Huerta-Diaz M.A. 2018. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications* 9: 246. doi: 10.1038/s41467-017-02446-8

Palmtag J., Ramage J., Hugelius G., Gentsch N., Lashchinskiy N., Richter A. and Kuhry P. 2016. Controls on the storage of organic carbon in permafrost soil in northern Siberia. *European Journal of Soil Science* 67: 478–491. doi: 10.1111/ejss.12357

Ramsay A.J. 1983. Bacterial biomass in ornithogenic soils of Antarctica. *Polar Biology* 1: 221–225. doi: 10.1007/BF00443192

Ramsay A.J. and Stannard R.E. 1986. Number and viability of bacteria in ornithogenic soils of Antarctica. *Polar Biology* 5: 195–198. doi: 10.1007/BF00446086

Roser D.J., Seppelt R.D. and Ashbolt N. 1993. Microbiology of ornithogenic soils from the Windmill Islands, Budd Coast. continental Antarctica: microbial biomass distribution. *Soil Biology and Biochemistry* 25: 165–175. doi: 10.1016/0038-0717(93)90023-5

Schuur E.A.G., McGuire A.D., Schädel C., Grosse G., Harden J.W., Hayes D.J., Hugelius G., Koven C.D., Kuhry P., Lawrence D.M., Natali S.M., Olefeldt D., Romanovsky V.E., Schaefer K., Turetsky M.R., Treat C.C. and Vonk J.E. 2015. Climate change and the permafrost carbon feedback. *Nature* 520: 171–179. doi: 10.1038/nature14338

Skrzypek G., Wojtuń B., Richter D., Jakubas D., Wojczulanis-Jakubas K. and Samecka-Cymerman A. 2015. Diversification of nitrogen sources in various tundra vegetation types in the High Arctic. *PLoS ONE* 10: e0136536. doi: 10.1371/journal.pone.0136536

Smith B.C. 2011. *Fundamentals of Fourier transform infrared spectroscopy*. CRC Press, Boca Raton.

Szymański W. 2017a. Chemistry and spectroscopic properties of surface horizons of Arctic soils under different types of tundra vegetation – A case study from the Fuglebergsletta coastal plain (SW Spitsbergen). *Catena* 156: 325−337. doi: 10.1016/j.catena.2017.04.024

Szymański W. 2017b. Quantity and chemistry of water-extractable organic matter in surface horizons of Arctic soils under different types of tundra vegetation – A case study from the Fuglebergsletta coastal plain (SW Spitsbergen). *Geoderma* 305: 30−39. doi: 10.1016/j.geoderma.2017.05.038

Szymański W., Skiba S. and Wojtuń B. 2013. Distribution, genesis, and properties of Arctic soils: a case study from the Fuglebekken catchment, Spitsbergen. *Polish Polar Research* 34: 289–304. doi: 10.2478/popore−2013−0017

Szymański W., Wojtuń B., Stolarczyk M., Siwek J. and Waścińska J. 2016. Organic carbon and nutrients (N, P) in surface soil horizons of Arctic soils from a non-glaciated catchment, SW Spitsbergen. *Polish Polar Research* 37: 49–66. doi: 10.1515/popore−2016−0006

Tatur A. 1989. Ornithogenic soils of the maritime Antarctic. *Polish Polar Research* 10: 481–532.

Tatur A. and Myrcha A. 1983. Changes in chemical composition of waters running off from the penguin rookeries in the Admiralty Bay region (King George Island, South Shetland Islands, Antarctica). *Polish Polar Research* 4: 113–125.

Tatur A. and Myrcha A. 1984. Ornithogenic soils on King George Island, South Shetland Islands (Maritime Antarctic Zone). *Polish Polar Research* 5: 31–60.

Watanabe T., Matsuoka N., Christiansen H.H. and Cable S. 2017. Soil physical and environmental conditions controlling patterned-ground variability at a continuous permafrost site. Svalbard. *Permafrost and Periglacial Processes* 28: 433–445. doi: 10.1002/ppp.1924

Wetterich S., Davidson T.A., Bobrov A., Opel T., Windirsch T., Johansen K.L., González-Bergonzoni I., Mosbech A. and Jeppesen E. 2019. Stable isotope signatures of Holocene syngenetic permafrost trace seabird presence in the Thule District (NW Greenland). *Biogeosciences* 16: 4261–4275. doi: 10.5194/bg-16-4261-2019

White D.M., Garland D.S., Ping C.-L. and Michaelson G. 2004. Characterizing soil organic matter quality in arctic soil by cover type and depth. *Cold Regions Sciences and Technology* 38: 63–73. doi: 10.1016/j.coldregions.2003.08.001

Wietrzyk-Pełka P., Rola K., Szymański W. and Węgrzyn M.H. 2020. Organic carbon accumulation in the glacier forelands with regard to variability of environmental conditions in different ecogenesis stages of High Arctic ecosystems. *Science of the Total Environment* 717: 135151. doi: 10.1016/j.scitotenv.2019.135151

Zawierucha K., Zmudczyńska-Skarbek K., Kaczmarek Ł. and Wojczulanis-Jakubas K. 2016. The influence of a seabird colony on abundance and species composition of water bears (Tardigrada) in Hornsund (Spitsbergen, Arctic). *Polar Biology* 39: 713–723. doi: 10.1007/s00300-015-1827-4

Zmudczyńska K., Olejniczak I., Zwolicki A., Iliszko L., Convey P. and Stempniewicz L. 2012. Influence of allochtonous nutrients delivered by colonial seabirds on soil collembolan communities on Spitsbergen. *Polar Biology* 35: 1233–1245. doi: 10.1007/s00300-012-1169-4

Zubrzycki S., Kutzbach L., Grosse G., Desyatkin A. and Pfeiffer E.-M. 2013. Organic carbon and total nitrogen stocks in soils of the Lena River Delta. *Biogeosciences* 10: 3507–3524. doi: 10.5194/bg-10-3507-2013

Zwolicki A., Zmudczyńska-Skarbek K.M., Iliszko L. and Stempniewicz L. 2013. Guano deposition and nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in Spitsbergen. *Polar Biology* 36: 363–372. doi: 10.1007/s00300-012-1265-5

Zwolicki A., Zmudczyńska-Skarbek K., Matuła J., Wojtuń B. and Stempniewicz L. 2016a. Differential responses of Arctic vegetation to nutrient enrichment by plankton and fish eating colonial seabirds in Spitsbergen. *Frontiers in Plant Science* 7: 1959. doi: 10.3389/fpls.2016.01959

Zwolicki A., Zmudczyńska-Skarbek K., Richard P. and Stempniewicz L. 2016b. Importance of marine-derived nutrients supplied by planktivorous seabirds to High Arctic tundra plant communities. *PLoS ONE* 11: e0154950. doi: 10.1371/journal.pone.0154950

Received 30 September 2022
Accepted 3 March 2023